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## Resurrection of *Scolopendra longipes* Wood and *Scolopendra cubensis* Saussure from synonymy with *Scolopendra alternans* Leach (Chilopoda, Scolopendromorpha, Scolopendridae): an enigmatic species-group needing phylogeographic analysis, with an overview on the origin and distribution of centipedes in the Caribbean region

RANDY J. MERCURIO

Eastern Research Group, Inc., Engineering and Science Division, 601 Keystone Park Drive, Suite 700, Morrisville, North Carolina 27560, U.S.A. E-mail: chilopods@yahoo.com

### Abstract

Resurrection of *Scolopendra longipes* Wood, 1862, and *Scolopendra cubensis* Saussure, 1860, from junior synonymy with *Scolopendra alternans* Leach, 1815, is proposed. A neotype specimen of *Scolopendra longipes* is designated. *Scolopendra longipes* has a restricted range from the Dry Tortugas up through the Florida Keys of Monroe County into the mainland Florida counties of Collier and Dade southeast to the Bahamas, while *Scolopendra cubensis* is endemic to Cuba. Characters distinguishing *S. longipes*, and *S. cubensis* from *S. alternans* are illustrated and compared using digital photography, micrography and morphometric data. It is suggested that what has been considered *Scolopendra alternans* from southern Florida through the Caribbean and into northern South America is probably an evolving species-group that has undergone major diversification sometime during the Paleocene and early Eocene ~65.5–50 million years ago (Ma), mainly due to geographic isolation caused by a combination of plate tectonics and 100,000 year cycles of glaciation/deglaciation.

**Key words:** Bahamas, Cuba, Florida, Greater Antilles, Haiti, Puerto Rico, Saba Island, vicariance, West Indies

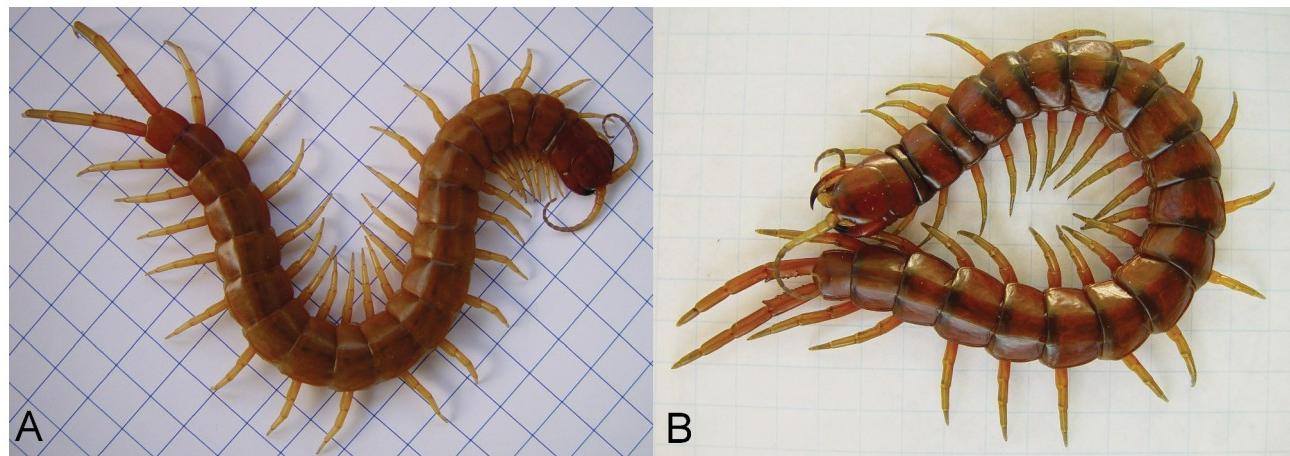
### Introduction

After obtaining live specimens of what were considered *Scolopendra alternans* Leach, 1815, from various localities through arthropod dealers, it was apparent that the general appearance of the animal from Florida (Figure 1A) always seemed remarkably different from those obtained from Haiti (Figure 1B) and Puerto Rico. This instigated a critical assessment of the taxonomic history of the species of *Scolopendra* found in these regions. A review of the literature on *Scolopendra longipes* Wood, 1862, and how it first became synonymized with *Scolopendra crudelis* Koch, 1847, and then both species with *S. alternans* is warranted.

Wood (1862) originally described *Scolopendra longipes* using five specimens. Three of these specimens were from Florida, one of which came from Ft. Jefferson, Garden Key, Dry Tortugas and the other two had no specific locality data. The two remaining, and largest, specimens Wood received were from Dr. J.B. Gilpin, which were labeled as being from Halifax, Nova Scotia. Wood stated that these specimens were “probably incorrectly labeled as to locality.” Perhaps these two specimens were obtained or found by Gilpin during his work for the Nova Scotian Institute of Science, where he had a strong interest in natural sciences and particularly fishes (Archives Canada, Virtual Museum Canada websites, see references). Dr. Gilpin may have spent a great deal of time near and around the Halifax harbor and these specimens were conceivably collected in the vicinity of the harbor as escapees or directly from a ship that incidentally transported them from Florida amongst cargo.

Just three years later Wood (1865) essentially repeated his 1862 publication with an English translation of his original Latin description. Porat (1876) was the first person to cite *S. longipes* as a synonym of *Scolopendra crudelis* Koch, 1847 but he provided no taxonomic discussion. Presumably following Porat’s synonymy, Meinert (1886), Underwood (1887) and Bollman (1893) continued citing *S. longipes* as a synonym of *S. crudelis*. Then

again, with no explanation for the synonymy, Pocock (1893) simply synonymized *S. longipes* and *S. crudelis* with *S. alternans*, which is where *S. longipes* has remained for more than 120 years. Probably following the synonymy of Pocock in 1893, Kraepelin (1903) then cited *S. crudelis* and *S. longipes* as synonyms of *S. alternans*. Incidentally, Pocock's synonymy of *S. crudelis* from St. Barthélemy with *S. alternans* was not justified and needs reevaluation.



**FIGURE 1.** Live dorsal habitus **A.** *Scolopendra longipes* from Florida, measuring 105 mm contracted and 120 mm extended. **B.** *Scolopendra alternans* from Haiti, measuring 140 mm contracted and 160 mm extended.

This trend of lumping poorly defined species from the Caribbean region under *S. alternans* has continued to the present day. However, Shelley (2002) recently cited *S. longipes* not only as a synonym of *S. alternans* but also mistakenly of *Rhysida longipes* (Newport, 1845), and included Wood's (1862) Florida locality record of Ft. Jefferson, Garden Key, as a published record for *R. longipes*, which actually belongs to *S. longipes*. Referring to Floridian records of *Rhysida*, Shelley & Edwards (2004) repeated Shelley's (2002) synonymy of *S. longipes* with *R. longipes*, and claimed "There is an old, uncorroborated record of *R. longipes* (Newport, 1845) from Fort Jefferson, Dry Tortugas National Park, Florida (Wood, 1862),..." although; under his discussion of *Rhysida*, Wood (1862) clearly states "This genus has not yet been found in N. America." Despite mistakenly considering the Ft. Jefferson record of *S. longipes* as one of *R. longipes* previously, Shelley (2006) again cited Wood's (1862) Ft. Jefferson record as a valid locality for *S. longipes*. In 2006, Shelley continued to cite *S. longipes* as a synonym of *S. alternans* and following Shelley's (2002) citation, Mercurio (2010) also cited *S. longipes* as a synonym of *S. alternans* and *R. longipes*.

The most obvious reason for this complication is that these two species have the same specific name. Secondly, not only is Wood's 1862 paper associated with the description of the new species *S. longipes*, but it is also where Wood proposes *Rhysida* to replace the preoccupied *Branchiostoma* for the African species *R. longipes*. Finally, *R. longipes*, or at least four species of this genus, have been encountered in quarantines at US ports since 1937 (Shelley, 2002) and a potentially established population has recently been found in Florida (Shelley & Edwards, 2004).

In the past, there has been some confusion as to the proper year assignment (1813 or 1815) for Leach's original description of *S. alternans*. *Scolopendra alternans* has been attributed to Leach's 1813 work in volume 7 of The Edinburgh Encyclopedia because in 1815, Leach cites his 1813 work as the original description for *S. alternans*, but the name has not been found in Leach's (1813) descriptions. In 2002, Shelley was unable to find Leach's Edinburgh Encyclopedia article and left the issue of the date unresolved. But in 2006, Shelley had seen a copy and stated that he was unable to find any mention of *S. alternans*, thus setting the publication date as 1815. Indeed, in his Edinburgh Encyclopedia article, *Crustaceology* (Leach, 1813), *Scolopendra alternans* is not mentioned, but Leach does describe a species under the name *Scolopendra inequalis*, a *nomen oblitum* which has never been used since (Bonato *et al.* 2005).

Leach (1813) described and categorized four *Scolopendra* species using three different body segment shape characters: 1) segments transversely quadrate (*S. spinipes* & *S. inermis*), 2) segments oblong-square (*S. morsitans*), and 3) segments alternately oblong and transversely quadrate (*S. iæqualis*). Leach's (1813) entire description of

*inæqualis* was “Segments alternately oblong and transversely quadrate. Sp. 4. *Inæqualis*. Segments rusty-brown; feet pale. Habitat unknown. *Scolopendra inæqualis*. Leach’s MSS.” An interpretation of the body segment description for *S. inæqualis* would be alternately longer than broad and broader than long, roughly square or rectangular. The fact that Leach (1815) cited himself in 1813 as his first description of *S. alternans* and that he used the word **alternately** to describe the body segments for *S. iæqualis*, he most likely renamed *S. iæqualis* as *S. alternans*, therefore, the forgotten name *S. iæqualis* is apparently the original name Leach used in 1813 for *S. alternans*. As Shelley (2006) concluded, the correct year for *S. alternans* is 1815 because this is when the name first appeared in the literature, and when the name was apparently changed from *S. iæqualis*.

In an attempt to verify the validity of the use of the junior synonym *S. alternans* over the senior synonym *S. inæqualis*, the Reversal of Precedence in Article 23.9 of the International Code of Zoological Nomenclature (ICZN) was consulted. The senior synonym *S. inæqualis* has not been used as a valid name after 1899 as is required by Article 23.9.1.1 of the ICZN. According to Article 23.9.1.2, if the junior synonym, *S. alternans*, has been used for a particular taxon as its presumed valid name in at least 25 works, published by at least 10 authors in the immediately preceding 50 years encompassing a span of not less than 10 years, then that name must replace the senior synonym, *S. iæqualis*. Evidence of such usage of *S. alternans* is provided by the following 25 publications: Bücherl 1974, Lewis 1981, Kevan 1983, Reger and Fitzgerald 1983, Carpenter and Gillingham 1984, Inchaustegui *et al.* 1985, Shelley and Edwards 1987, Lewis 1989, Behan-Pelletier 1993, Loesel *et al.* 2002, Shelley 2002, Dial and Roughgarden 2004, Shelley and Chagas 2004, Lewis *et al.* 2005, Shelley 2006, Strausfeld *et al.* 2006, Laboy-Nieves 2009, Mercurio 2010, Wu *et al.* 2011, Perfetti 2012, Shelley and Sikes 2012, Undheim *et al.* 2012, Vahtera *et al.* 2012, Barro and Cherva 2013, Reveal, 2013; therefore, *S. alternans* is a *nomen protectum* and prevails over the senior synonym *S. inæqualis* under Article 23.9 of the ICZN.

If one were to look at a specimen of *S. longipes* or *S. cubensis*, and were only looking for those major characters that define *S. alternans*, one would quickly conclude they were *S. alternans*. In the years since Porat (1876) synonymized *S. longipes* with *S. crudelis*, and Pocock (1893) synonymized *S. longipes* and *S. crudelis* with *S. alternans*, the differences among these three species have never been carefully reevaluated. Moreover, the synonymy of *S. cubensis* with *S. alternans* by Kraepelin (1903) has not been scrutinized either. According to Hollier (2015, pers. comm., 23 November) Kraepelin (1903) examined the syntypes of *S. cubensis* before synonymizing it with *S. alternans* but he gave no explanation for doing so. Attems (1930) thought that *S. cubensis* was perhaps a synonym of *S. alternans* but didn’t cite Kraepelin’s (1903) synonymy.

The goal of this study was to determine if the Floridian *S. longipes* is indeed a distinct species from *S. alternans* populations found on the Greater Antillean islands of Hispaniola and Puerto Rico. Below, *S. longipes* is redescribed and restored to species status, *S. cubensis* is also given species status, and an analysis of the characters that help to differentiate these species from what is considered *S. alternans* in the Caribbean region is presented. To bring much needed attention to the perplexing biogeography of the centipede fauna in the Caribbean region, possible explanations for their likely origin and distribution are reviewed.

## Material and methods

A total of 92 *Scolopendra* specimens were used in this study. Sixteen of the specimens were obtained from dealers as live individuals, some being subsequently preserved, and 76 specimens were either loaned by the United States National Museum (USNM), California Academy of Sciences (CAS), Museum of Comparative Zoology (MCZ), Field Museum of Natural History (FMNH) or studied at the American Museum of Natural History (AMNH). Due to the poorly preserved condition of some of the museum material, not all specimens were used for certain measurements. Nine wild-caught live *Scolopendra longipes* from Florida were purchased during 2012–2013 from Swift Invertebrates (SI) and Glades Herp Farm, Inc. (GHF, which has since closed). These centipedes are sold in the pet industry and have various common names, such as Caribbean Giant, Florida Giant and Florida Keys Centipede. One adult *S. longipes* specimen obtained from SI in early November 2012 expired for unknown reasons not long after a successful molt in mid-September 2013; it was preserved and used for the micrographs. Two live *Scolopendra alternans* from Haiti were purchased in 2013 through Tarantulaspiders.com (TS). It is not known exactly where two preserved Haitian *S. alternans* were obtained; however, they were found to be consistent with other material from Haiti. Two preserved *S. alternans* specimens from Puerto Rico were obtained through a private importer in 2001. One preserved *Scolopendra longipes* from the Bimini Islands was purchased from GHF in June

1998. All material not belonging to museums that were used for this study remain in the author's private collection (RJM Collection) with the exception of the *S. longipes* specimen from Florida used in the morphological photos, which will be deposited at the USNM. Locality information for the material examined is followed by the number of specimens from each locality and the institution abbreviation in parentheses. Due to the fact that this study could not resolve all species within the *alternans*-complex, all references to *S. alternans* s.l. from different localities are potentially distinct species from each other and from *S. alternans* s.s. as described by Leach.

Digital photographs were taken with a Sony DSC-F707, Cyber-shot 5 megapixel digital still camera with a non-detachable Carl Zeiss Vario-Sonnar lens system. Habitus images were taken without a flash in natural daylight using 6.35 mm (0.25 inch) square graph paper as the background to provide scale. Micrographs were taken with the same camera coupled to a Bausch & Lomb StereoZoom 4 microscope using a ScopeTronix MaxView™ Plus microscope adapter. One microscope eyepiece was fitted with a 10 mm reticle for measurements. A Dolan-Jenner Industries Fiber-Lite, model LMI 6000 with dual gooseneck fiber optic light guides and focusing lenses were used for illumination. Image of sensillia trichodea taken using reflected light with above light source and camera coupled to a Leitz Laborlux II microscope. Images were cropped, labeled and scale bars created using GNU Image Manipulation Program (GIMP) version 2.6. Using GIMP, coloration nomenclature was derived using the average of 10 random RGB measurements from each region of interest from digital photographs of each species and matched to a digitized version of Ridgway's (1912) color plates, which were measured in the same fashion for comparison.

A clear plastic tube with a cap was used to weigh specimens and take body length measurements of living specimens. Weights of live specimens were taken with a Mettler Toledo four place balance (model AG104) and final measurements were rounded to the nearest tenth of a gram. Living specimen body length measurements are given in a range because their trunk can be contracted or extended. The maximum lengths and widths of the ultimate prefemora were taken looking dorsally as illustrated in Figure 2A. The prefemoral process was not included in any of these measurements. The maximum widths of the ultimate prefemora were taken at the widest point in dorsal view, not including the spines, the prefemoral process or any curvature associated with either that deviated from the overall width of the article. Only one ultimate prefemur was measured from each animal and any legs that appeared to be regenerated were not measured. The prefemur length was compared to body size for all species using the prefemur width as a proxy to control for any allometric change. Anatomical terminology follows that of Bonato *et al.* (2010). Language translations of original descriptions were assisted by the use of Google Translate.

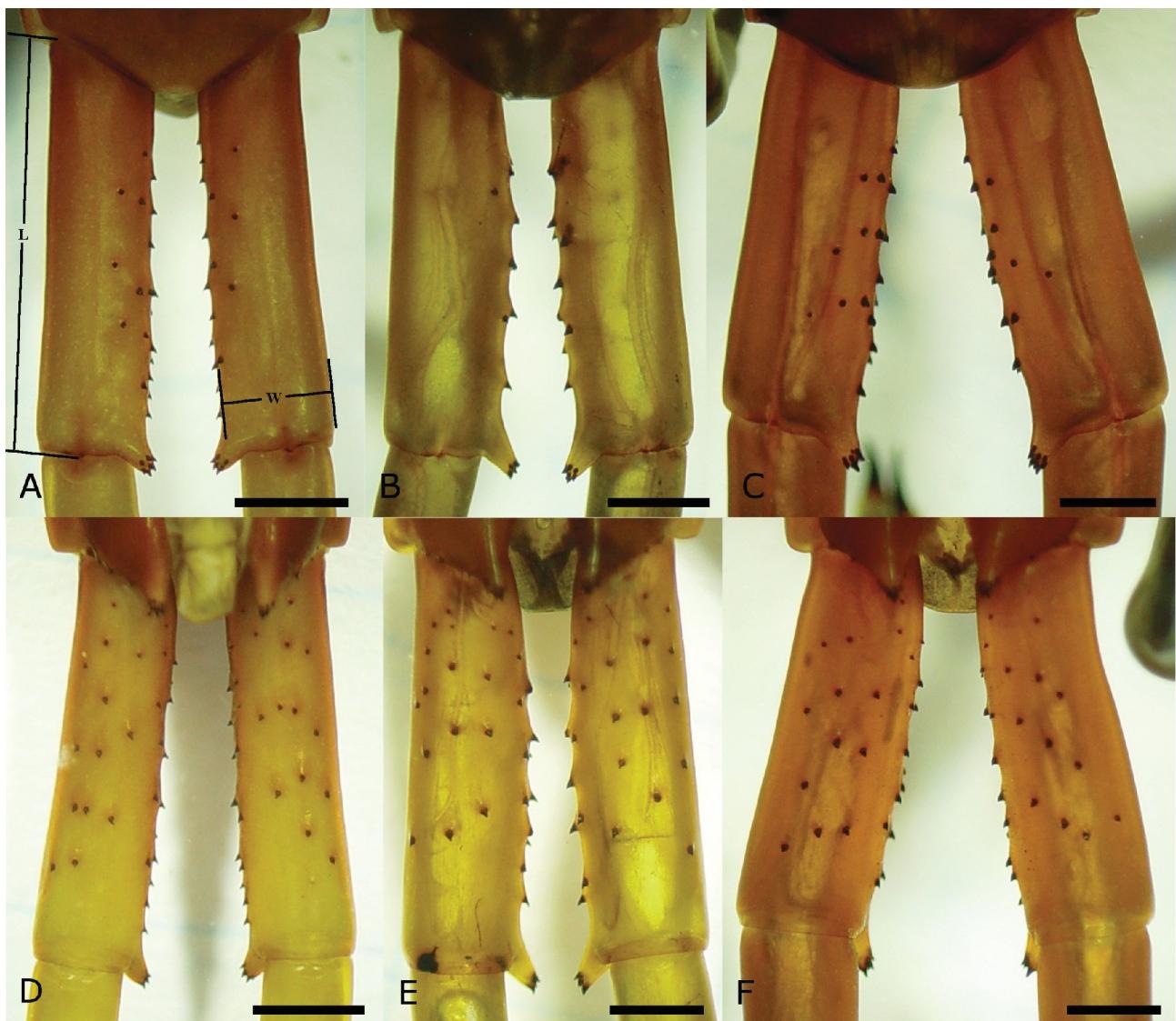
## Results

### *Scolopendra longipes* Wood, 1862 Revalidated

(Figs. 1A, 2A, D, 3, 4 A–B, 5A, 6 A–B, 7 A–B, 8; Table 1)

*Scolopendra longipes*—Wood, 1862: 26 (nec *S. alternans* Pocock 1893, nec *S. alternans* Kraepelin 1903, nec *S. alternans* Chamberlin 1914, nec *S. alternans* Attems 1930, nec *S. alternans* Shelley 2002, nec *S. alternans* Mercurio 2010).

**Type locality.** The original type locality should be: USA: Florida, Ft. Jefferson, Garden Key, Dry Tortugas, received by Wood from Dr. D.D. Whitehouse, measuring 115 mm; however, the type material for *S. longipes* cannot be found at the USNM despite the fact that Wood states all of the listed specimens belonged to the Smithsonian Institution. After reading Roth's (1959) biographical memoir on Wood it was discovered that while Wood's original manuscript of *The Myriapoda of North America* was waiting for publication it was destroyed by a fire on January 24, 1865 at the Smithsonian. Unfortunately, it is highly likely that the type material for *S. longipes* was also destroyed during this fire. As far as can be ascertained, no original type material exists, therefore I designate the following type: **NEOTYPE:** Unknown sex from Florida, Monroe Co., Sugar Loaf Key, 2.7 miles S. of junction U.S. RTE 1 and FLA 939 (at sugar loaf channel, on NE end of island) on FLA 939, 24°37'28.3"N 81°31'06.6"W, 15 March 1977, 1400 hrs., sunny, 86°F, S. Blair Hedges, col., Under moist cardboard lying on the ground in the shade of a mangrove tree on the Atlantic side of Rte. 939 (1, USNM), measures 98 mm. At some point a topotype should be obtained and genetically compared to a specimen from this neotype location to assure that this topotype specimen is not a subspecies.

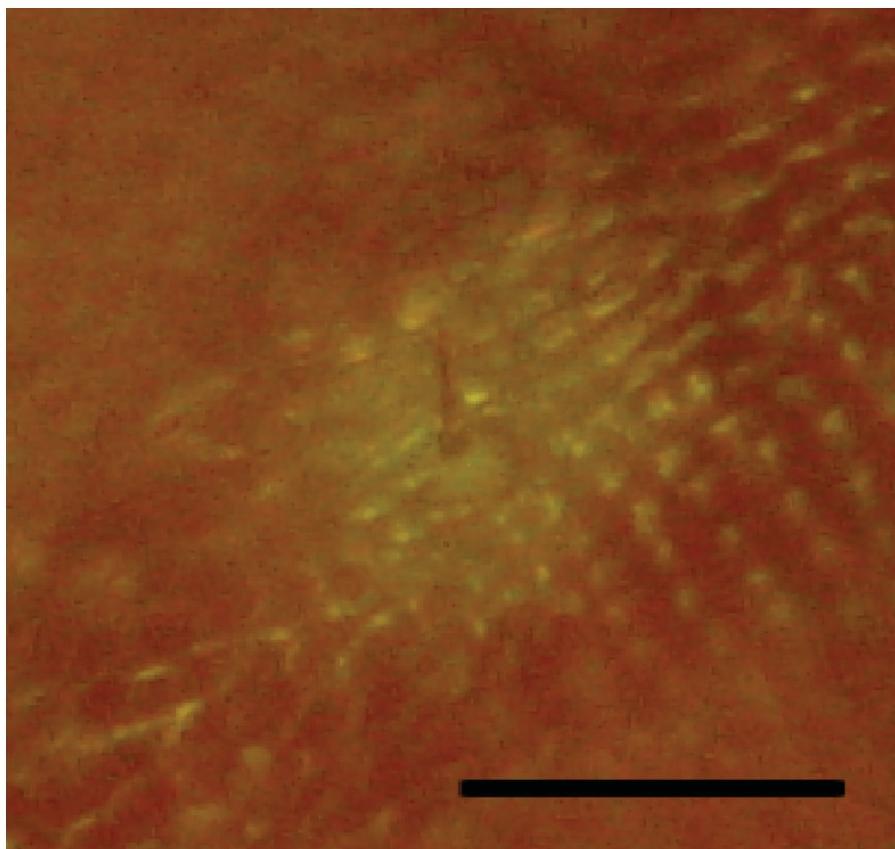


**FIGURE 2.** Ultimate prefemora, dorsal **A.** *Scolopendra longipes*, Florida **B.** *Scolopendra alternans*, Haiti **C.** *Scolopendra alternans*, Puerto Rico; Ultimate prefemora, ventral **D.** *Scolopendra longipes*, Florida **E.** *Scolopendra alternans*, Haiti **F.** *Scolopendra alternans*, Puerto Rico (Scale bars = 2 mm).

**Material examined.** Bahama Islands: N. Bimini, Feb. 17, 1970, V. Roth, (1, AMNH); South Bimini, May, 1951, W.J. Gertsch & M.A. Cazier, (2, AMNH); South Bimini, May, 1951, Gertsch & Cazier, (2, AMNH); So. Bimini, No. Shore, Jan. 1, 1952, (1, AMNH); west end of South Bimini Island, under rotten palm log, Sept. 26, 1947, James Oliver, (1, AMNH); Bimini, Oct. 6, 1947, James Oliver, (1, AMNH); Nassau, New Providence, May 31, 1904, W.W. Wheeler (A3245, Cat. No. 1542), (1, AMNH); Nassau, New Providence, West Bay, May 29, 1904, W.W. Wheeler (A3246, Cat. No. 1541), (1, AMNH). Bimini, obtained from GHF in 1998 (1, RJM). USA: Florida, Key Largo, Feb. 25, 1906, S.A. Binion (A3339, Cat. No. 1563), (1, AMNH); Monroe Co., Boot Key, April 1, 1996, R. Lawson & P.G. Frank (2, CAS); Miami, July, 1918 Mus. Exped., W.I. Charlesworth col., Rec'd from Dept. of Botany, Aug. 15, 1922 (3, FMNH); Monroe Co., Plantation Key, 4 mi. S. of Tavernier, 11.III.1963, H.L. Levi, edge hardwood forest, (1, MCZ); Monroe Co., Little Torch Key: L9/15, 28.i.79, Coll. J. Lazell (1, MCZ); Monroe Co.; No Name Key; 1.1 miles E., 0.25 miles S. Bogie Channel Bridge, 16 Jan 1978, 0930 hrs., ca. 57°F, under trash, S. Blair Hedges (1, USNM); Monroe Co., No Name Key, 1.5 miles E. Bogie Channel Bridge, 16 Jan 1978, 1000 hrs., ca. 60°F, under cardboard, S. Blair Hedges (1, USNM); Monroe Co.; Largo Key, ca. 6.3 miles NNE Key Largo (2.5 miles N. jct. RTE 1 on FLA. 905) 14 January 1978, 1730 hrs., ca. 62°F, under trash on east side of RTE 905, S. Blair Hedges (1, USNM); Chapman Field, Sept. 1928 (1, USNM); Monroe Co., Sugar Loaf Key, 2.7 miles S. of junction U.S. RTE 1 and FLA 939 (at sugar loaf channel, on NE end of island) on FLA 939, 15 March 1977, 1400

hrs., sunny, 86°F, S. Blair Hedges, col., Under moist cardboard lying on the ground in the shade of a mangrove tree on the Atlantic side of Rte. 939 (1, USNM); Florida, obtained from SI on November 6, 2012 (2, RJM); Florida, obtained from SI on November 7, 2013 (6, RJM).

**Redescription.** This redescription is based on live and preserved specimens observed, and is not drawn from a single specimen. Length up to 152 mm. Figure 1A illustrates the overall body shape and coloration in life. The cephalic plate, 1<sup>st</sup> tergite, forcipular segment and tergites 20–21 are burnt sienna. The burnt sienna color may continue further towards the middle of the trunk from 1<sup>st</sup> tergite and 20<sup>th</sup> tergite, but the midsection of the trunk generally appears lighter varying from russet to tawny. In recently preserved specimens (70–75% ethanol), the trunk tends to blend into a uniform tawny while the head and forcipular segment remain a burnt sienna.



**FIGURE 3.** Sensilla trichodea from ultimate tergite of *S. longipes*, Florida (Scale Bar = 50 µm).

Antennal segments 16–18, with 17 being the most common. The first five antennal segments are glabrous with the remaining distal segments being hirsute. The cephalic plate is slightly longer than wide with a median ratio of 1.06 and a range of 1.01–1.09. The lateral margins of the head gently converge anteriorly, posterior edge rounded, paramedian sutures complete and diverging anteriorly, and sparsely punctate (~3–4/mm<sup>2</sup>) with punctuation due to *sensilla trichodea*. These *sensilla trichodea* are very conspicuous over the entire body (Figure 3). The three medial teeth of coxosternal tooth-plate are fused, with or without pronounced invagination between the second and third teeth (Figures 4A–B). The forcipular tergite lacks an anterior transverse suture but has complete paramedian sutures and these continue through tergite 20. Excluding the questionably large specimens, the maximum tergite width was 9.2 mm, which occurred on the 10<sup>th</sup> tergite. The ultimate tergite lacks a medial longitudinal suture (Figure 5A). Sternite 2 has incomplete paramedian sutures beginning anteriorly and appear to end approximately 1/3 the sternite length with very faint continuation, if any, posteriorly. Sternites 3–20 have complete paramedian sutures and appear more pronounced posteriorly. The posterior edge of the ultimate sternite is gently rounded to rounded with the latter seemingly more common in smaller specimens (Figures 6A–B). Tarsus one of leg one with a dorsal anterior spur and legs 1–20 each with a ventrodistal spur. The eighteenth prefemur of left or right leg may rarely have a single spine on the distomedial process. The antepenultimate prefemur usually has two spines on the distomedial process; but sometimes only 1 may be present. The penultimate prefemur has 4–6 spines on the

distomedial process and typically 1–2 spines on dorsomedial surface (Figures. 7A–B). The dorsomedial spines of the penultimate prefemur on younger specimens may vary slightly from what is seen in most specimens, such as two on left and none on right. Older specimens may show an additional spine on left or right, such as three on left and two on right. The ultimate prefemoral process typically has 6–8 spines with 7 being the most common. The maximum length to maximum width of the ultimate prefemur has a median ratio of 3.75, with a range of 3.65–3.95 (Figure 8). The total spine count on the ventral, medial, and dorsal surfaces of the ultimate prefemur ranges from 28–37, excluding the distomedial process. The coxopleural pores are either uniformly minute with a smooth appearance, as in *S. alternans* (Figures. 6C–D), to a mixture of small and minute pores giving a rough appearance (Figures. 6A–B). The lateral coxopleural spines are typically two, with three on occasion; and the third being closer to the coxopleural process, which typically has 7–10 spines.

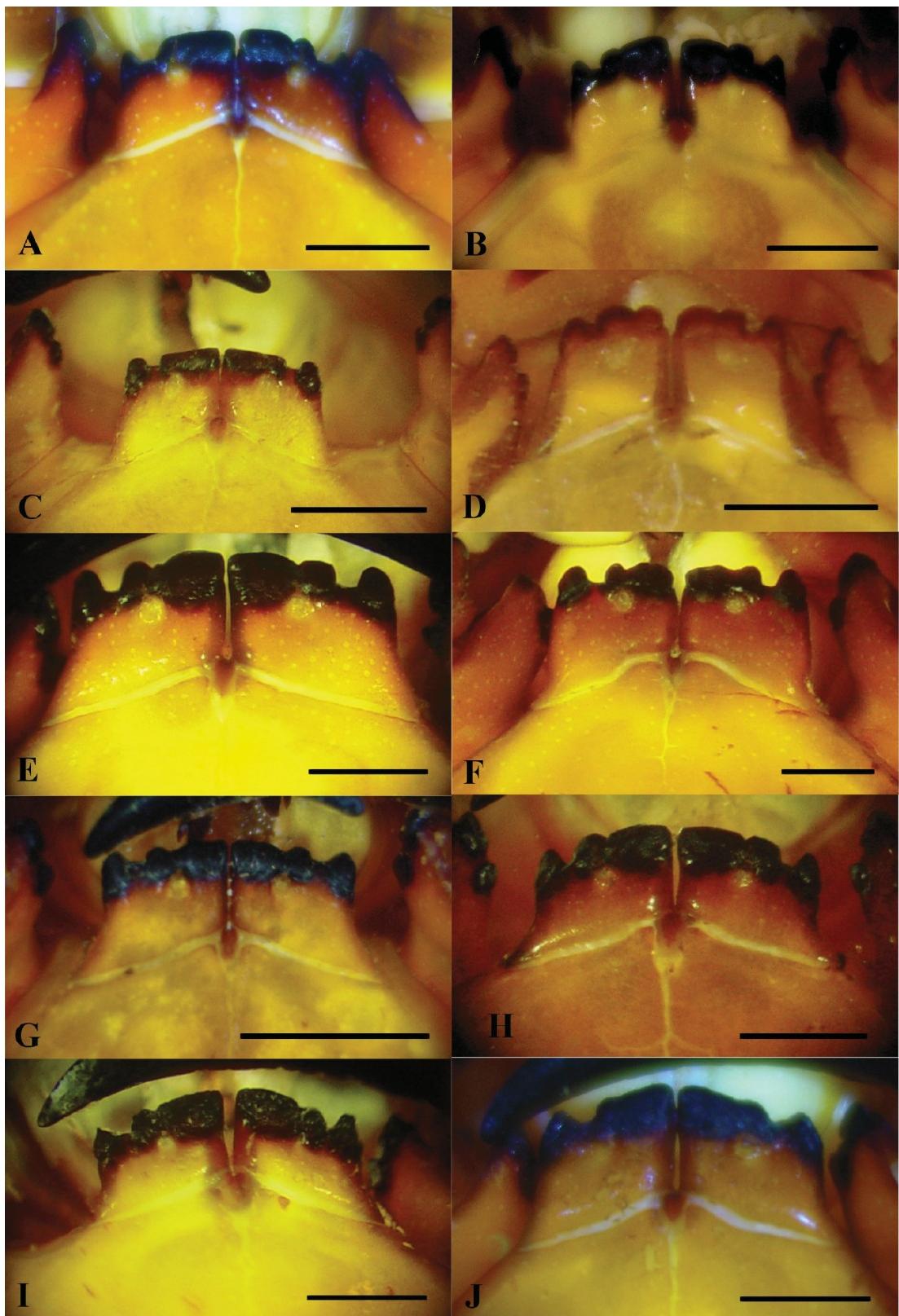
**Geographical distribution.** From Dry Tortugas through Florida Keys and southern Florida including the counties of Monroe, Dade and Collier, to the Bahamas.

**Etymology.** The specific name *longipes* means long-foot and refers to the long, thin ultimate legs found in *S. longipes*.

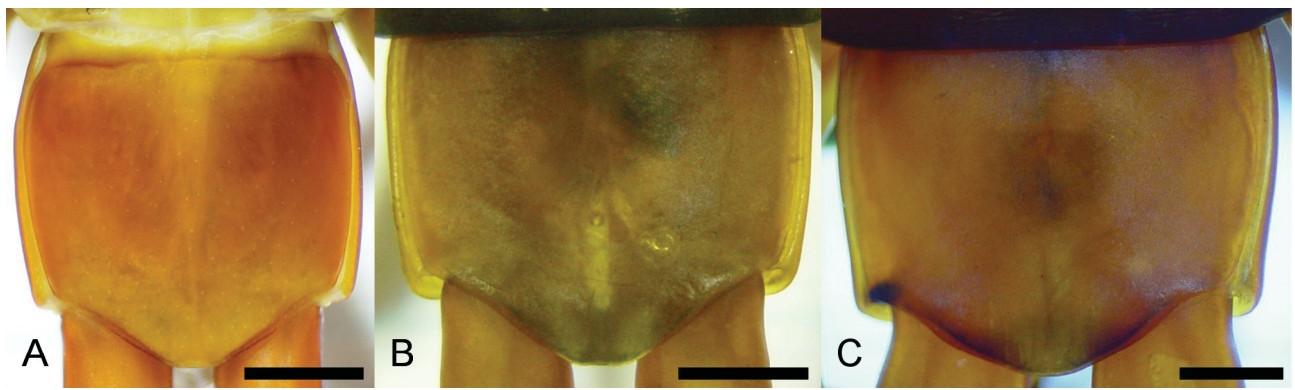
**Remarks.** Evidently the description of *S. longipes* by Wood has never been thoroughly reviewed by subsequent authors, because there is one difficult-to-see character he mentions that clearly differentiates *S. longipes* from *S. alternans*. In Wood's (1865) English description he clearly states, "...basal joint of penultimate pair armed with 5 spines on a terminal angular process and 1–2 others;" Wood's "basal joint" actually refers to the penultimate prefemur. Therefore, the key differentiating characters here are the 1 or 2 other spines, because his language strongly suggests he was not indicating 1 or 2 additional spines on the prefemoral process but was actually referring to the spines found on the dorsomedial surface of the penultimate prefemur.

Wood (1862, 1865) mentions three characters of *S. longipes* that differ from Newport's (1844, 1845) characters of *S. alternans*. Firstly, the process of the forcipular trochanteroprefemur (which Wood called the "mandibular tubercle" and Newport referred to as the "mandibular tooth.") was claimed by Wood to be "...very large and having the lesser tubercle near to its base..." and Newport described the "...mandibles strong, with the tooth small, but armed with a minute tubercle near its apex..." The process of the trochanteroprefemur in *S. longipes* and *S. alternans* appears very similar and when taking variability into account does not provide good characters to distinguish these two species. Secondly, Wood stated that the number of spines on the prefemur of the ultimate pair of legs was 30–45 in *S. longipes* but 45–60 in *S. alternans*. Specimens of *S. alternans* with anywhere near a total of 60 spines on the ultimate prefemur were not observed in this study. Newport was very clear in stating that 30–40 spines were on the dorsal and medial surfaces while 15–20 were on the ventral surface. The maximum number of spines seen on the dorsal and medial surfaces combined in *S. alternans* is 21 in addition to 17 on the ventral, but this is another character that is fraught with difficulty because it is frequently hard to determine if a spine should be labeled as dorsal/medial or medial/ventral. Perhaps a standardized method of describing the positions of the ultimate prefemur spines can be derived, but at the moment a foolproof way of assessing these spines in the *S. alternans*-complex is elusive. Newport said the locality for his specimens of *S. alternans* was "Caribbean Islands," which is highly indefinite, but this difference in spines on the ultimate prefemur suggests he may not have been looking at a specimen from Florida, Cuba, Haiti or Puerto Rico. Therefore, the 40–60 spines on the ultimate prefemur of *S. alternans* as opposed to the 30–45 in *S. longipes* cannot be corroborated as a good character to separate these species. Finally, referring to the ultimate coxopleuron of *S. longipes*, Wood mentions the roughness of the "lateral anal appendages". He was surely referring to the ultimate coxopleura of *S. longipes*, which can have an evenly distributed pattern of variably sized, small to minute coxal pores (Figures 6A, B) giving a rougher look than those of *S. alternans*, with uniformly sized minute coxal pores, evenly distributed, and a smoother appearance (Figure 6C, D). It should be noted that specimens of *S. longipes* from various Florida Keys have uniformly minute pores giving a rather smooth appearance, similar to what would be considered *S. alternans*. This coxopleural pore variability, along with other variable characters and extended periods of isolation on relatively small islands, suggests that *S. longipes* may also actually be composed of subspecies. Incidentally, the diameter and surface area density of these coxopleural pores may be useful distinguishing characters, as well as that of the *sensillia trichodea*.

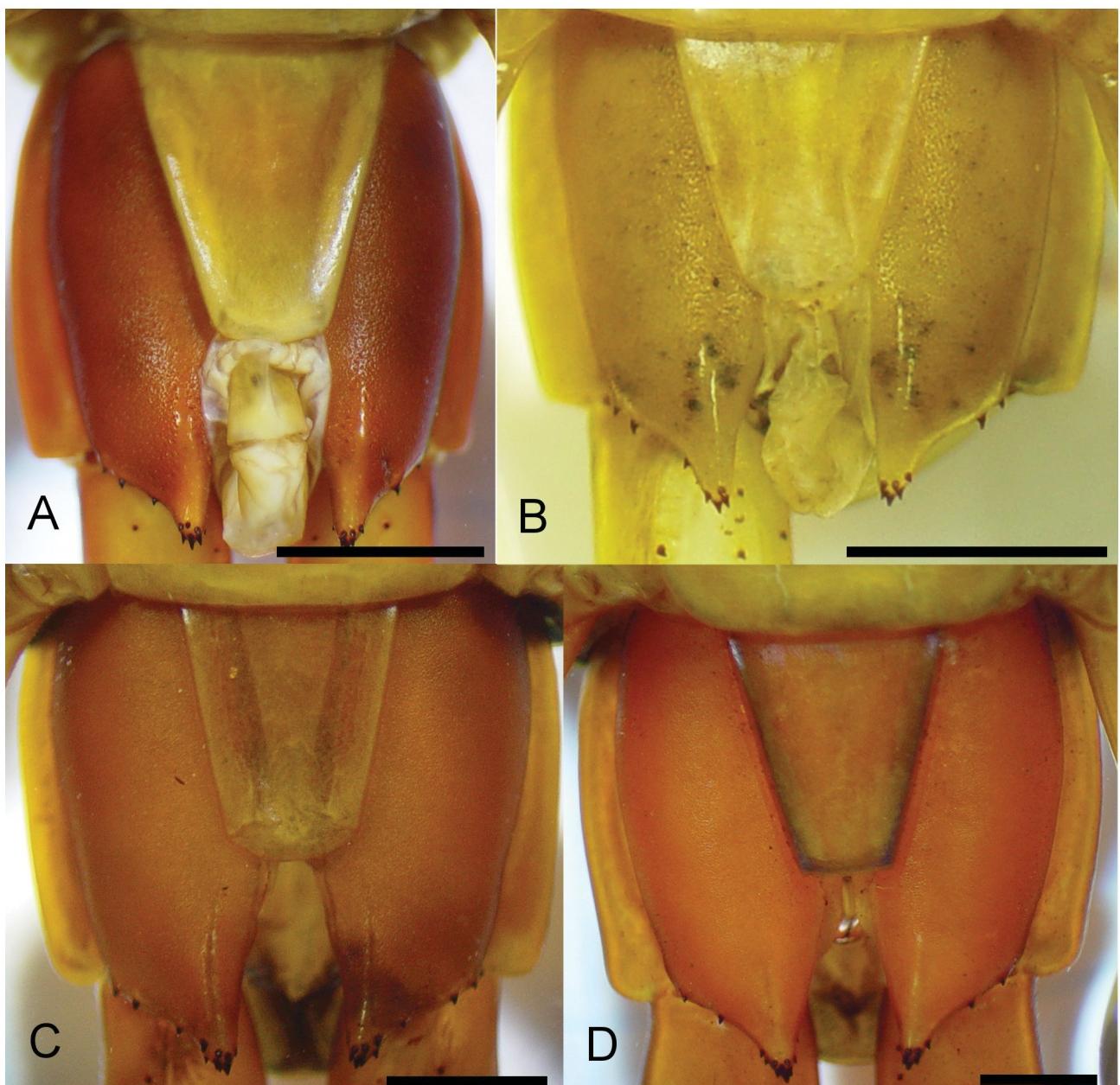
The range in length of the five specimens of *S. longipes* that Wood (1862) reported was 95.25–127 mm. In living specimens of *S. longipes*, the maximum adult length and weight ranges observed in this study were 105–128 mm and 5.3–6.4 g respectively. The longest specimen was from Chapman Field, Miami, which was about 152 mm but was poorly preserved.



**FIGURE 4.** Coxosternal tooth-plate, ventral **A.** *S. longipes*, Florida, RJM Collection **B.** *S. longipes*, Florida, Sugar Loaf Key, USNM, Neotype **C.** *S. cubensis*, Cuba, Matanzas, USNM **D.** *S. cubensis*, Cuba, El Guama, USNM **E.** *S. alternans*, Haiti, Planisance, USNM **F.** *S. alternans*, Haiti, Trou Caiman, USNM **G.** *S. alternans*, Dominican Republic, Santo Domingo, USNM **H.** *S. alternans*, Puerto Rico, RJM Collection **I.** *S. alternans*, Puerto Rico, Mayagüez, FMNH **J.** *S. alternans*, Saba Island, FMNH (Scale Bars = 1 mm).

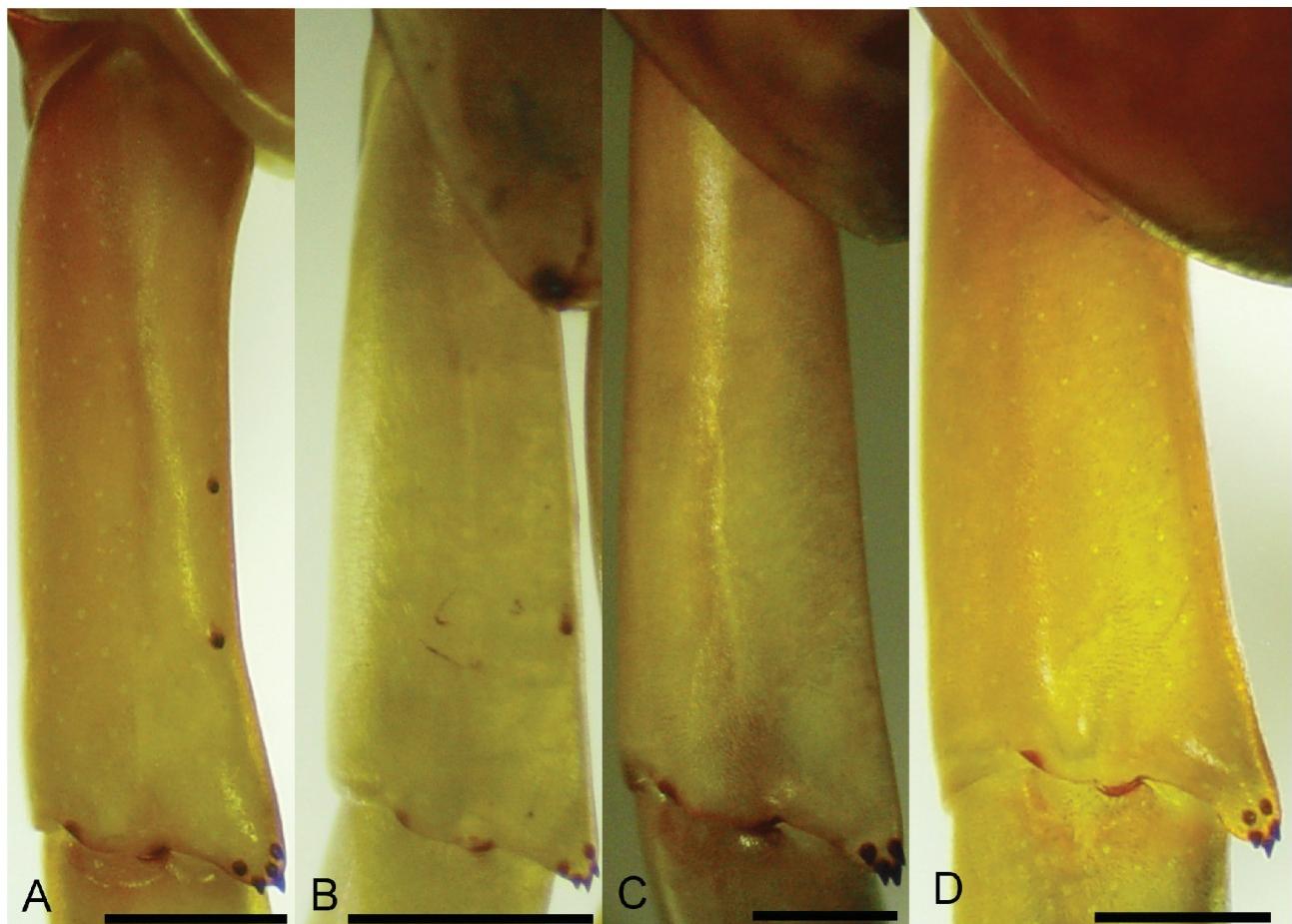


**FIGURE 5.** Ultimate tergites, dorsal **A.** *Scolopendra longipes*, Florida **B.** *Scolopendra alternans*, Haiti **C.** *Scolopendra alternans*, Puerto Rico (Scale bars = 2 mm)



**FIGURE 6.** Ultimate pedal segment, ventral **A.** *Scolopendra longipes*, Florida **B.** *Scolopendra longipes*, Bimini **C.** *Scolopendra alternans*, Haiti **D.** *Scolopendra alternans*, Puerto Rico (Scale bars = 2 mm).

During the course of this study, three of the live *S. longipes* laid eggs and brooded between 30–43 offspring. Although most of them were raised, some didn't survive and were preserved. After examining four offspring from one female, only one specimen had a single faint spine on the right dorsomedial surface of the penultimate prefemur. This indicates that these spines are added with age, so they may not typically be present on specimens that are  $\leq 30$  mm long. Two of the juvenile specimens that were well preserved had an ultimate prefemur length to width ratio of 3.82, which was consistent with that of the adults. The Bimini Island specimen is young and has 1 dorsomedial spine on each penultimate prefemur (Figure 7B). The two smaller live specimens of *S. longipes* from Florida (~100 mm), which are a little larger than the Bimini specimen (~75 mm), also have one dorsomedial spine on both penultimate prefemurs. Based on the material examined in this study, the addition of the second dorsomedial spine (distal) on each penultimate prefemur of *S. longipes* appears to occur with age.



**FIGURE 7.** Left penultimate prefemur, dorsal **A.** *Scolopendra longipes*, Florida, **B.** *Scolopendra longipes*, Bimini **C.** *Scolopendra alternans*, Haiti **D.** *Scolopendra alternans*, Puerto Rico (Scale bars = 1 mm).

#### *Scolopendra cubensis* Saussure, 1860 Revalidated (Figs. 4C–D, 8; Table 1)

*Scolopendra cubensis*—Saussure, 1860: 129 (nec *S. alternans* Kraepelin 1903, nec *S. alternans* Attems 1930, nec *S. alternans* Shelley 2002, nec *S. alternans* Mercurio 2010).

**Type locality.** Cuba. The Natural History Museum of Geneva (MHNG) has 3 syntypes.

**Material examined.** All specimens USNM. Cuba: Matanzas, 1937, Kriuitsky, 148187, 785-10,130 (3); Loma La Canoa, 1937, Kriuitsky, 148187, 847-11,209 (7); San Diego de los Baños, April 22, 1900, Palmer & Riley, 102 (2); Havana, 1937, Kriuitsky, 148187 (1); El Guama, March 24, 1900, Palmer & Riley (1).

**Remarks.** *Scolopendra cubensis* should now be recognized as a valid species based on the different length to

width ratio of the ultimate prefemur and smaller maximum body length as shown in figure 8 and table 1. Saussure (1860) described *Scolopendra cubensis* from Cuba with no other specific locality data. According to Hollier & Hollier (2012), Saussure was in Cuba from January 29, 1855 to February 22, 1855 and visited Havana, Guanabacoa, Santa Maria del Rosario, Matanzas and Limonar; therefore, the type series was most likely collected during this time period and from one of these localities. Saussure's (1872) French description of the coxosternal tooth-plate for *S. cubensis* was translated as follows: "...four strong teeth each side, usually seen with two blades having a wavy edge, one in which at least two internal are fused; sometimes only has three lobes on each side, indicating only three teeth; but the outer teeth are generally somewhat more clearly outlined than others." Ventral view images of the coxosternal tooth-plates of the three syntypes for *S. cubensis* were found to be consistent with observations of the Cuban material in this study, such as the Matanzas specimen illustrated in figure 4C, but the exception was the single specimen from El Guama shown in figure 4D. Although the length to width ratio of the ultimate prefemur for the El Guama specimen was not at either extreme and close to the median, these coxosternal tooth-plate differences hint that intra-island variation of *S. cubensis* may exist.

The distomedial tubercle of the penultimate prefemur has 3–5 spines, with four being the most common, and five of 13 specimens had one dorsomedial spine on one penultimate prefemur. The El Guama specimen, which overall seemed to be slightly different from the other material examined, had one faint dorsomedial spine on both penultimate prefemora.

**TABLE 1.** Major morphological characters that differentiate *S. longipes* and *S. cubensis* from *S. alternans*. Bolded numbers indicate the most common spine combinations observed.

	<i>S. longipes</i> Florida/Bimini	<i>S. cubensis</i> Cuba
Coloration	<b>cephalic plate, forcipular segment &amp; tergites 20, 21:</b> burnt sienna; <b>trunk:</b> russet to tawny without posterior black transverse band on tergites; <b>legs:</b> aniline yellow (living coloration)	<b>cephalic plate &amp; forcipular segment:</b> appear darker in coloration than rest of trunk with posterior black transverse band on tergites (preserved)
Maximum Length (mm)	152 ( <i>n</i> =22)	95 ( <i>n</i> =12)
Penultimate Prefemur	<b>1/1, 1/2, 2/0, 2/1, 2/2, 3/2</b>	<b>0/0, 0/1, 1/0, 1/1</b>
Dorsomedial Spines (Left/Right)	( <i>n</i> =21)	( <i>n</i> =13)
Median ultimate prefemur length/width	3.75 ( <i>n</i> =21)	2.89 ( <i>n</i> =13)

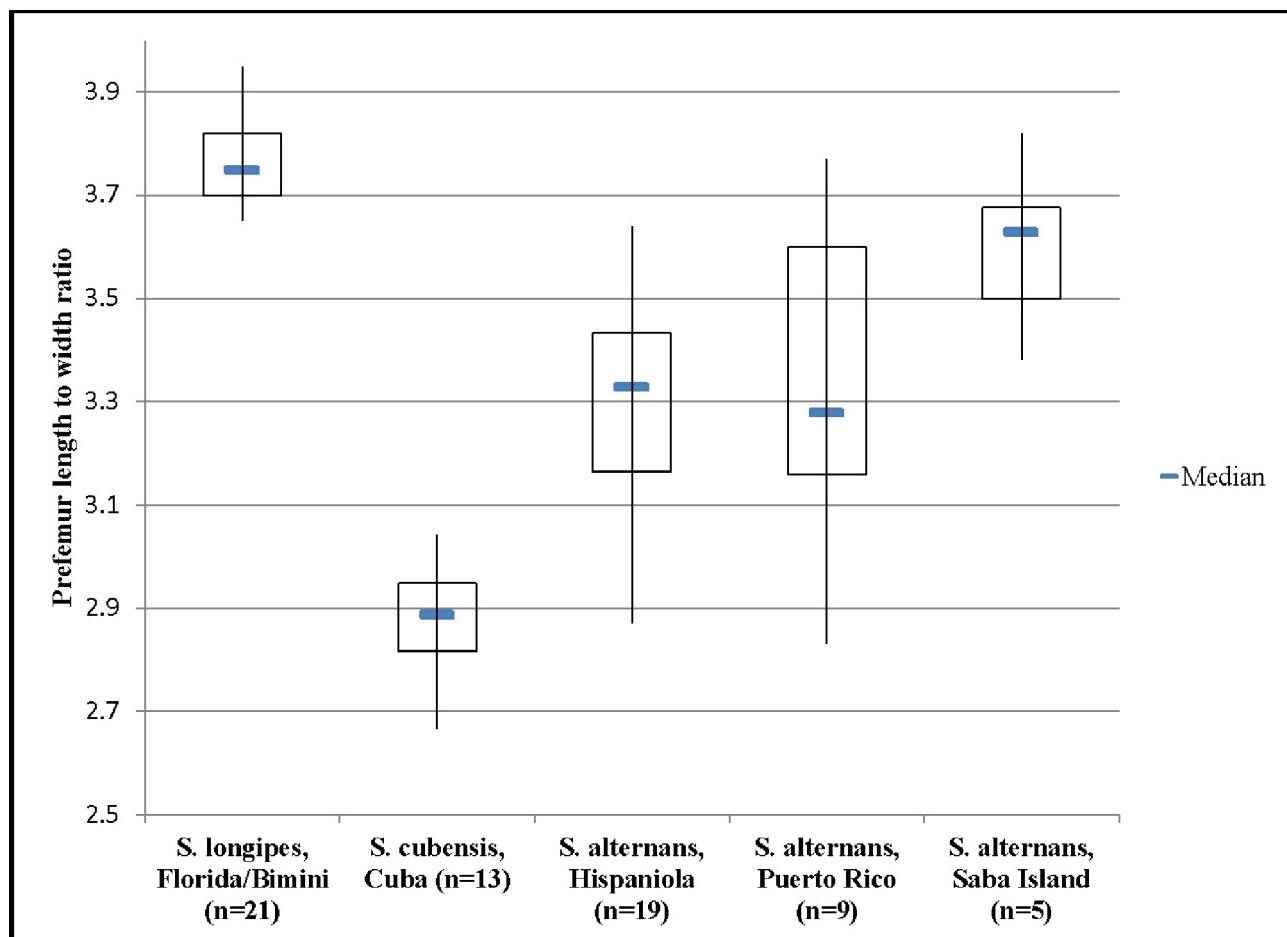
continued.

	<i>S. alternans</i> Hispaniola	<i>S. alternans</i> Puerto Rico	<i>S. alternans</i> Saba Island
Coloration	<b>cephalic plate through tergite 21:</b> uniform antique brown to English red with posterior black transverse band on tergites; <b>legs:</b> sulphine yellow (living coloration)	<b>cephalic plate through tergite 21:</b> uniform antique brown to English red with posterior black transverse band on tergites (preserved)	<b>cephalic plate &amp; forcipular segment:</b> appear darker in coloration than rest of trunk with posterior black transverse band on tergites (preserved)
Maximum Length (mm)	176 ( <i>n</i> =17)	134 ( <i>n</i> =10)	138 ( <i>n</i> =19)
Penultimate Prefemur	<b>0/0, 0/1, 1/0, 1/1, 2/1</b>	<b>0/0, 0/1, 1/0</b>	1/1, 2/1
Dorsomedial Spines (Left/Right)	( <i>n</i> =19)	( <i>n</i> =10)	( <i>n</i> =5)
Median ultimate prefemur length/width	3.33 ( <i>n</i> =19)	3.28 ( <i>n</i> =9)	3.63 ( <i>n</i> =5)

According to Saussure (1860, 1872), the two body lengths of *S. cubensis* he gave were 73 and 92 mm, respectively, and all of the material examined was 73–95 mm. The specimen from Havana was poorly preserved, in 4 pieces and measured 106 mm long but was not included in the maximum length data as it was felt to be biased high. One of the specimens from Matanzas was missing the ultimate segment; hence there were only 13 of 14

specimens used for calculating the length to width ratios of the ultimate prefemora and 12 of 14 used for maximum body length. The median length to width ratio of the ultimate prefemur was 2.89 and ranged from 2.67–3.04 (Figure 8). All of the above material from Cuba has been tentatively labeled as *S. cubensis*, but it is anticipated that it will take more morphometric and molecular data to help determine if there is more than one species on the island of Cuba. Due to the limited availability of material and realizing the potential for insular variation of *S. cubensis*, a redescription at this time is not possible.

Another species currently recognized as a junior synonym of *S. alternans* is Gervais's (1837) *Scolopendra sagræa*, which has Cuba as a type locality, but seems to be a larger species than *S. cubensis*, attaining a body length of 144 mm.



**FIGURE 8.** Boxplot illustrating the difference in the ultimate prefemur length to width ratio of *S. longipes* compared to *S. cubensis* and *S. alternans* from different regions.

#### *Scolopendra alternans* Leach, 1815

(Figs. 1B, 2 B–C, E–F, 4 E–J, 5B–C, 6C–D, 7C–D, 8; Table 1)

*Scolopendra alternans*—Leach, 1815: 408 [Type locality: unknown, see discussion below].

**Type locality.** Leach (1813) stated that the habitat was unknown for *S. iæqualis* and in 1815 and 1817 Leach had no habitat listed for *S. alternans*. The original type specimen and the locality for *S. alternans* remains unknown (see Shelley, 2002). Unable to find a type specimen for *S. alternans*, Shelley (2002) designated a neotype for the species from the British Virgin Islands because Leach was British, and he felt the type may have come from a British territory in the Caribbean. **NEOTYPE:** British Virgin Islands, Tortola, Fat Hog's Bay, 12 March 1984 collected by A. Penn. The neotype specimen has not been examined for this study and Shelley did not provide any illustrations or morphological details. The suitability of this neotype specimen should be reevaluated in the future in light of the hypothesis that *S. alternans* records represent a species group rather than a single species.

**Material examined.** Dominican Republic: East of La Romana, north of large sugar plantation, under rocks along road in humid forest, N 18.29.443 W 68.55065, ele: 208 ft., coll: J. Huff, July 2004 (1, AMNH); Dominican Republic: Azna, Sto. Domingo, 3-13-13, P.G. Russel (1, USNM); Santo Domingo, Colegio De La Salle, Bro. Basilio Augusto (1, USNM); Boca del Inferno, Samana & B., Feb. 29, 1928 (1, USNM); Haiti, Lake Assuei, Mar. 11, 1918 (1, USNM); Etang Saumâtre, April 6, 1920, Dr. W.L. Abbott (1, USNM); Planisance, Nov.–Mar. 1925, caught eating large snail, Coll. E. C. Leonard (1, USNM); Trou Caiman, Feb. 18, 1943, A. Curtiss (5, USNM); Haiti (4, RJM); Puerto Rico: Mayagüez, June 21, 1948, J.A. Rivero (2, FMNH); San Juan, Nov. 3, 1899, on battlement under old bricks, Coll. Cook, Collins, Gall? (2, USNM); San Juan, 1899, August Busck (1, USNM); Lares, January 25, 1899, August Busck (2, USNM); Cayey, June 1902, D.M.C.? (1, USNM); Puerto Rico (2, RJM); N. Antilles: Saba Island, Windward side, Elev. 400 m, Jan. 13–15, 1968, B. Malkin (20, FMNH).

**Remarks.** In 1815 and 1817, Leach listed *S. alternans* as a species with the general characters of “Corporis segmenta transversa alternantia, quinto et sexto subæqualibus,” which translates to body segments transversely alternating, 5<sup>th</sup> and 6<sup>th</sup> subequal. The maximum length of *S. alternans* is on the order of 150–190 mm (Shelley 2002). The maximum adult length and weight observed in this study for live *S. alternans* from Haiti ~150 mm long and weighed ~10.7 g.

The coxosternal tooth-plates exhibit some fairly consistent variation from region to region (Figure 4E–J). There are differing degrees of medial teeth fusing, where the invagination takes place between teeth (sometimes differing in the same specimen on either side of the tooth-plate), and the extent which the medial teeth protrude beyond that of the outer teeth. The leading edges of the teeth vary from blunt, crushing, molar-like as that in the Haitian, Trou Caiman specimen (Figure 4F), while those with piercing and sharp knife-like edges are seen in the Puerto Rican, Mayagüez specimen (Figure 4I). Tooth-plate structure is perhaps indicative of the preference for a particular prey item, where the need for crushing, piercing or slicing is more appropriate for puncturing or opening their prey to gain access to the more easily imbibed liquid contents. Overall, the anterior borders of tooth-plates show some subtle but noticeable variability throughout the Caribbean region. For example, the anterior tooth-plate border of the *S. alternans* specimen from Mayagüez, Puerto Rico is more curved with the fused, medial teeth protruding well beyond the lateral teeth (Figure 4I), when compared with that of the *S. cubensis* specimens from Matanzas, Cuba, whose anterior tooth-plate border is only slightly curved (Figure 4C). When viewed ventrally, there is some noticeable intra-island variation of the tooth-plates within close proximity to one another. A good example of this is observed in the tooth-plate of the *S. alternans* specimen from Planisance, Haiti, when compared with that of the *S. alternans* specimen from Trou Caiman, Haiti (Figures 4E, F, respectively). Notice the lateral tooth-plate edges of the specimen from Planisance consistently slope laterad moving posteriorly, where as that of the Trou Caiman's has a region near its base that is incurved. Preliminary data for coxosternal tooth-plates hold promise for morphological characters such as the ratio of the maximum length of median embayment to leading edge of teeth to the distance between coxosternal condyles; as well as the overall structure, sclerotization, and fusing of coxosternal teeth but large specimen series are needed to do a statistical analysis.

In *S. alternans* from Puerto Rico the posterior edge of the ultimate tergite has heavier sclerotization (Figure 5C) than that for *S. longipes* or *S. alternans* from Haiti. Sternites 2–20 in the Haitian *S. alternans* have complete, rather pronounced, paramedian sutures. Sternites 2–10 in the Puerto Rican *S. alternans* have incomplete paramedian sutures, 11–20 complete with the intensity of the sutures slightly increasing posteriorly. As it is in *S. longipes*, the posterior edge of the ultimate sternite in *S. alternans* from Haiti is gently rounded to rounded (Figure 6C). The ultimate sternite of *S. alternans* from Puerto Rico has a very gently rounded to straight posterior edge, and also exhibits a dark colored border (Figure 6D), which does not appear in *S. longipes* or in the specimens from Haiti.

The boxplot in figure 8 shows the median length to width ratio of the ultimate prefemur for *S. alternans* from Hispaniola at 3.33, *S. alternans* from Puerto Rico at 3.28 and *S. alternans* from Saba Island at 3.63. Two small specimens from San Juan, Puerto Rico have ultimate prefemora whose length to width ratios are close to the low range of *S. longipes* but they have no dorsomedial spines on the penultimate prefemora. The maximum width of the ultimate prefemur occurs distally in *S. longipes* and the Puerto Rican *S. alternans*, but in the Haitian specimens it was located medially where it is crassate and shows more pronounced spination (Figures 2A–F).

It should be noted that a series of specimens from Trou Caiman, Haiti always exhibited at least 1 dorsal spine on the left and right, with one specimen having 2 on one left penultimate prefemur but the length to width ratio was always less than that of *S. longipes*, was overall stockier looking and had similar coloration like that of the live

Haitian specimen in figure 1B. The Etang Saumâtre specimen exhibited a mottled pattern on the head and tergites, which was unique.

Lewis (1989) studied 9 specimens of what he identified as *S. alternans* from St. John (U.S. Virgin Islands). Three things from his study provide further evidence for inter-island variation: 1) all 9 specimens ranged from 20–69 mm in length, which is a rather small body length range considering these specimens were collected in two different years in the months of February, March, May and October; 2) the color description ranging from olive to dark brown is dissimilar to the rusty-brown color of *S. alternans* 3) in his figure 2, the paramedian sutures are incomplete on the cephalic plate and absent from tergite 1. Although this suggests that the animal from St. John may be distinct from *S. alternans*, it is possible that these were all juveniles, and if so, this would further indicate that there is a need for detailed studies of character variation in different growth stages. Furthermore, Lewis (1989) observed variations in the margination of the tergites from the St. John *S. alternans* specimens and correlated it to body length. Perhaps there is also some variation in tergite widths and patterns with age and gender.

Shelley (2002) synonymized *Scolopendra hirsutipes* Bollman, 1893 with *S. alternans* by process of elimination, based on the lack of an anterior transverse suture on tergite 1 and spur counts of the ultimate legs. According to Shelley, the holotype of *S. hirsutipes* cannot be found at the USNM, but the description alone, with a lack of cephalic plate sulci and 25–27 antennal segments suggests it is not *S. alternans*. Bollman (1893) did cite the habitat of *S. hirsutipes* as “West Indian fauna”; however, because he thought all other unlabeled material in this particular collection seemed to be from Surinam that the *S. hirsutipes* specimen may have also been from Surinam.

The original description of Koch’s (1847) *Scolopendra crudelis* from St. Barthelemy was based on two specimens he said were very different in color from each other. One was said to be pale yellow ochre and the other a rusty-red with yellow legs. Due to this fact, there is a good chance this species was described from two different species and should not be considered a synonym of *S. alternans* until the types and/or fresh material can be studied. He stated that the ultimate prefemur had 24–26 spines in 7 uninterrupted rows on the ventral and medial surfaces. This is slightly less than the 28 observed on a few specimens in this study. Although Meinert (1886) listed Florida as the locality for a specimen of *S. crudelis* he described from Double Headed Shot Key, this island is now considered part of the Bahamas and is about 60 nautical miles southeast of the Florida Keys. His description of *S. crudelis* is much closer to matching the population of *S. alternans* from Haiti than it is to *S. longipes*. Perhaps it is conspecific with a population from Cuba, but because the medial part of the ultimate prefemur is described as rounded and the total body length as 150 mm, it is unlikely to be *S. longipes*.

There is certainly no overlap of the length to width ratio of the ultimate prefemur with *S. longipes* and *S. cubensis*, or the *S. alternans* of Saba Island with *S. cubensis*, but the populations of Hispaniola and Puerto Rico certainly need further resolution. It is obvious that general morphological characters of *S. alternans* do not make it easy to differentiate the species present in the Caribbean region. Nonetheless, minute details of some of the morphological evidence from this preliminary investigation of the *S. alternans*-complex point to a highly diverse fauna throughout the Caribbean region. Although further study of the *S. alternans* species-group is beyond the scope of this paper, an overview of factors presented below convey the possible origins of the Caribbean centipede fauna and why *Scolopendra alternans* is a species-group rather than a single species.

**Origin and distribution.** Pereira *et al.* (1997) mentioned that “...the most puzzling element of the Neotropical fauna of Geophilomorpha is constituted by the large non-endemic genera whose distribution cannot be explained within the usual framework of old Gonwanian elements or recent Northern immigrants.” Foddai *et al.* (2004) reiterated that our knowledge of the Neotropical Geophilomorpha is limited. The entire centipede diversity found in the Caribbean region remains relatively understudied. The fauna’s origin is enigmatic because it is not known how the islands were colonized nor is it clear how the *S. alternans* species-group radiated over such an enormous geographical area. We do know that most Old World *Scolopendra* lack an anterior transverse suture on their first tergite. Therefore, the presence of at least 3 *Scolopendra* species, *S. longipes*, *S. cubensis* and *S. alternans*, in the Neotropics without a transverse suture suggests this closely related group evolved from a Gondwanan relict. The existence of such relicts is supported by the work of Moran and Smith (2001) on phytogeographic relationships between Neotropical and African-Madagascan pteridophytes. In addition, the presence of the predominantly African genus *Ballophilus* Cook (1896), with two species in South America and one in Puerto Rico, is also an indicator of a probable Gondwanan component.

By simply analyzing known distributions of some geophilid genera (*Ityphilus* Cook, 1899; *Polycricus* Saussure and Humbert, 1872; *Telocricus* Chamberlin, 1915 and *Titanophilus* Chamberlin, 1915), the scolopendrid genus

*Newportia* Gervais, 1847 and two scutigerid genera (*Dendrothereua* Verhoeff, 1944 and *Sphendononema* Verhoeff, 1904) in the southern Nearctic and Neotropical region, we observe that the Greater and Lesser Antillean chilopod fauna consists of Central and South American components. The expansive distribution and diversity of these various chilopod representatives in southern Florida, Central and South America, as well as throughout the Greater and Lesser Antilles suggests that they most likely colonized these areas through a land-bridge.

Whether the Greater and/or Lesser Antilles were ever connected to North, Central and/or South America, and how, has been and remains very controversial (e.g. MacFadden 1980, Iturralde-Vinent and MacPhee 1999, Graham 2003, Hedges 2006, Ali 2012, Alonso *et al.* 2012). Nevertheless, there are three main theories that could explain how the terrestrial fauna of the Greater and Lesser Antilles arrived:

- 1) over-water dispersal and rafting have been suggested methods of island colonization for centipedes in the Caribbean region (Shelley, 2002; Shelley & Sikes, 2012);
- 2) the Greater Antilles + Aves Ridge land-bridge hypothesis dubbed GAARlandia by Iturralde-Vinent and MacPhee (1999) where the Aves Ridge connected northern South America with the Greater Antilles somewhere between 35–33 Ma;
- 3) the tectonic reconstruction model of the Caribbean region by Pindell and coauthors (e.g. Pindell and Barrett 1990, Pindell 1994, Pindell and Kennan 2009, Pindell *et al.* 2011), which suggests that the proto-Antillean arc was connected from Mexico to South America starting ~130 Ma through ~59 Ma.

In regards to over-water dispersal and rafting, there is no reason to believe that this can't happen; however, it most likely consisted of limited events. For example, Heatwole and Levins (1972) found a dead centipede on a piece of flotsam within 16 km of Puerto Rico, but all of the flotsam they found about 120 km from the nearest land lacked terrestrial animals. Iturralde-Vinent and MacPhee (1999) stated that: "...surface-current dispersal of propagules is inadequate as an explanation of observed distribution patterns of terrestrial faunas in the Greater Antilles." Furthermore, Fritsch and McDowell (2003) also concluded that more than one biogeographical scenario is required to account for the current distribution and biology of the Antillean flora.

The main difference between the two remaining theories is when the land emerged and became colonizable. Although both of these scenarios may have occurred and are possible explanations, the latter tectonic model provides the most credible explanation for the initial origin of the centipede fauna seen in the Greater/Lesser Antilles and southern Florida for the following three reasons:

1) Near the end of the existence of the inter-American land bridge created by the proto-Antillean arc as suggested by Pindell *et al.*, 2011, around 65.5 Ma, the Chicxulub asteroid impacted the Yucatan Peninsula and caused a world-wide mass extinction (Schulte *et al.* 2010). Although Graham (2003) suggested that the initial period during which the Greater Antilles became available for colonization by terrestrial flora and fauna was ~49 Ma in the Middle Eocene, this time-period was after the Antillean arc had separated from the continents based on Pindell's model. It seems reasonable that biota would have radiated sooner into the proto-Antillean arc, immediately after the Chicxulub asteroid impact, while it was still connected to Central and South America.

2) The diverse presence of the predominant Central American *Polycricus* (Geophilomorpha: Geophilidae) throughout the Greater and Lesser Antilles suggests that these species or their ancestors were most likely in existence on the Antillean arc before it separated from Central America, and that at least some parts of the Greater Antilles remained emergent during glacial minima for their persistence.

3) According to Pindell (1994) there was a Bahamian-Antillean collision termination in the middle Eocene, which could explain the presence of *S. longipes* in southern Florida and the Bahamas.

Since the effective colonization of the Caribbean region by centipedes, ongoing cyclical selective pressures have been created through glacial maxima and minima affecting sea levels. Fleming *et al.* (1998) postulated that somewhere between 16,000 and 7,000 years ago the ocean levels rose from about 100 meters less than they are today to within 3–5 meters of today's. Yokoyama *et al.* (2000) concluded that the Last Glacial Maximum (LGM) was between 22,000 and 19,000 years before present. According to Abe-Ouchi *et al.* (2013) these glacial cycles are primarily driven by insolation cycles that last ~100,000 years, with a saw-toothed pattern of gradual growth and fast termination. Their data indicates that the global sea-levels may have dropped by as much as 120 m during the LGM. Even with the current sea floor depths in the Caribbean region, if the ocean level were dropped by 120 m it would seemingly not create any land-bridges connecting North, Central or South America to the Greater Antilles. Although glacial maxima and minima don't seem to explain the biogeography of centipedes in the Caribbean or

even how *S. longipes* arrived in southern Florida, it may have assisted the *S. alternans* species-group to radiate via land-bridges throughout the Greater and Lesser Antilles during times of glacial maxima.

## Conclusions

This study creates a preliminary foundation suggesting that inter-island variation exists among what is considered *Scolopendra alternans* for the Caribbean region. As far as can be determined from this rudimentary morphological study, *S. longipes* is a valid species endemic to southern Florida and the Bahamas, and *S. cubensis* is also a valid species from Cuba. While morphological evidence suggests that *S. longipes* and *S. cubensis* are closely related to *S. alternans*, the latter is in need of much further investigation to help resolve what appears to be a morphologically cryptic species-group. Even with the limited material used in this study, insular populations from Cuba, Hispaniola and Puerto Rico exhibited slight morphological variation where subspecies recognition may be necessary. Besides *S. alternans*, no other single centipede species is known to inhabit the entire Caribbean region. For this reason, it is proposed that *S. longipes* in Florida and the Bahamas, together with *S. cubensis* from Cuba and the broad range of what is currently called *S. alternans* in the Caribbean and South America should be tentatively recognized as the *S. alternans* species-group.

We are getting closer to understanding that the observed centipede diversity seen in the Caribbean region today is due to a combination of many factors. It seems probable that tectonic processes causing geographic isolation in combination with selective pressures, as a result of glaciation cycles, provides a plausible explanation as to why there are slight variations in what has been considered *S. alternans* throughout the Caribbean region. Referring to the biogeography of terrestrial vertebrates in the Antilles, Pregill and Olson (1981) summarized this nicely stating: “The alternate exposure and submergence of land, and the correlated alternation of xeric and mesic environments, would have resulted in repeated events of faunal isolation, speciation, and extinction, such that relict distributions would be superimposed on one another as a mosaic through time.”

The taxonomy of scolopendromorphs is being revolutionized by molecular genetic evidence at the family and genus level (e.g. Vahtera, Edgecombe & Giribet 2013). Furthermore, Bond & Sierwald (2002, 2003) demonstrated that species of rhinocricid millipedes on the island of Jamaica were morphologically cryptic, and were able to decipher clades through the 16S rRNA gene of the mitochondrion. The numerous species described by various authors in the past that are now considered synonyms of *S. alternans* need a complete, combined morphological and molecular reevaluation based on preserved and fresh material collected from the entire range of what is considered *S. alternans*. The time has come to apply molecular techniques to determine just how diverse *Scolopendra* is in the Caribbean region. A phylogeographic study is encouraged to determine the extent of inter- and intra-island differentiation of the *S. alternans* species-group. Perhaps we can then use the *S. alternans*-complex as a centipede model to unravel the mysteries of how they adaptively radiated throughout the Caribbean.

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